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Early Development Drives Variation in Amphibian Vulnerability to Global Change

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Understanding how natural selection determines species' life histories can reveal their resilience or sensitivity to anthropogenic changes. For example, the safe harbor hypothesis posits that natural selection will favor life histories that maximize the time spent in the safest life stages; a second theoretical prediction suggests that species with complex life histories will maximize the growth potential of a life stage relative to its safety. Amphibians exhibit complex life histories, with a diversity of developmental strategies occurring across taxa. Many strategies involve the complete elimination of a particular life stage, and thus provide an excellent opportunity to evaluate the main tenets of the safe harbor hypothesis and understand the consequences of this developmental variation for conservation of threatened amphibians. We develop a general framework for understanding developmental life histories of amphibians – including the special cases of paedomorphism, direct development, and viviparity – based on the relative growth potential and safety offered by aquatic and terrestrial habitat, which we tested using a global trait database. We then compare the IUCN Red List status of species differing in developmental mode, revealing that most fully aquatic species and species with an aquatic larval stage are currently of Least Concern, despite the fact that freshwater habitats are being lost at a much faster rate compared with terrestrial ecosystems. The higher proportion of direct developing and viviparous species that are threatened can be attributed to their smaller ranges, the fact that they are more likely to be found in rainforest habitats, and their relatively slow life histories. We conclude that an amphibian's developmental mode reflects the relative costs and benefits of different habitats, and that this could contribute to the resilience or vulnerability of amphibians to future anthropogenic change.

Keywords: IUCN Red List, life histories, paedomorphosis, viviparity, safe harbor hypothesis, direct development

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INTRODUCTION

Amphibians are known both for their diversity of life histories and for the alarming fact that a greater proportion of amphibian species are threatened with extinction than any other vertebrate group (Duellman, 1989; Stuart et al., 2004; Wells, 2007; Hoffmann et al., 2010; IUCN, 2021). Previous work has addressed the relative vulnerability of amphibian taxa with different life histories to anthropogenic threats, including climate change, disease, and habitat loss (Becker and Loyola, 2008; Loyola et al., 2008; Becker et al., 2010; Lourenço-de-Moraes et al., 2019). But the unique diversity of amphibian life cycles has not been integrated into standard indices of intrinsic productivity that are frequently used to characterize extinction (Hutchings et al., 2012; Foden et al., 2013; Zhao et al., 2018; He et al., 2021).

The strategies that amphibians have evolved in response to different ecological pressures, given developmental constraints in each lineage, offer a unique window into how species are likely to cope with ongoing environmental change arising from human influences. Although a life history that spans both aquatic and terrestrial environments is most common in amphibians, there are notable exceptions where a species has evolved to specialize on one habitat or the other, and the origin of this diversity in life cycles is not fully understood (Istock, 1967; ten Brink et al., 2019). There are numerous independent examples across the three amphibian orders where a particular developmental stage has been completely omitted, offering a rich opportunity for comparative study (Salthe, 1969; Salthe and Duellman, 1973; Duellman, 1989; Kupfer et al., 2016). Direct development has arisen independently in frogs, salamanders, and caecilians, and involves eliminating the aquatic larval stage in favor of terrestrial egg deposition; progeny complete metamorphosis within the egg (Wells, 2007; Kupfer et al., 2016; Lion et al., 2019). At the opposite end of the spectrum, several salamander lineages exhibit paedomorphosis, remaining fully aquatic throughout life.

The origin and maintenance of these diverse developmental modes in amphibians can be understood in the context of different risk-reward trade-offs experienced in aquatic and terrestrial habitats. The amount of time each species spends in each life stage – which may, at its extreme, mean an entirely aquatic or entirely terrestrial life history – reflects the evolutionary conditions that have generated the remarkable diversity of life histories in amphibians (Werner, 1986; Duellman, 1989). As we will discuss, aquatic habitats can be ephemeral or predictable, risky or safe, and nutritionally rich or poor, relative to their adjacent terrestrial habitats. Here, we argue that understanding the ecological and evolutionary forces that have shaped the life-history diversity of the three amphibian orders offers new insight into differences among species in their risk of extinction.

In this paper we propose a framework based on classic theory to predict how selective forces have shaped the diversity of amphibian life histories, which can generate novel insights into their vulnerability to global change. We highlight disparities in the IUCN Red List status among species with different developmental modes, and that species which have presumably evolved to increase the relative safety of early life stages are more likely to be categorized as threatened. We then explore the connection between developmental mode, species range size, biogeography, and intrinsic sensitivity to anthropogenic threats. Our framework is the first to incorporate the complexity of the full spectrum of amphibian life histories when assessing their relative extinction risk by including their exposure to different threats in different habitats. We suggest this approach can inform global conservation efforts, raise unanswered questions regarding amphibian reproductive strategies, and prioritize future research directions.

A FRAMEWORK FOR PREDICTING HOW SELECTIVE FORCES SHAPE AMPHIBIAN LIFE HISTORIES

The strategy selection system assumes life-history strategies are shaped by particular characteristics of the environment (Southwood, 1988). The overall strategy of an organism is optimized in a given environment by selective forces operating on a suite of fitness-related traits (Southwood, 1988; Roff, 2002). Abiotic and biotic pressures experienced in a given environment will determine the optimal life-history strategy in that environment, and anthropogenic change that alters abiotic and biotic conditions could lead to the evolution of new life-history strategies (which may include shifts to different environments; ten Brink et al., 2020), and/or population declines and extinction (**Figure 1**). For species with complex life cycles the relative likelihood of these outcomes is dependent upon (1) the strength of phylogenetic inertia, (2) the extent and rapidity of environmental change, and (3) the relative impact of alterations to the habitats utilized by each life stage.

The typical amphibian life cycle consists of a gelatinous egg, deposited in the water, an aquatic larval stage, and a terrestrial adult form following metamorphosis (Duellman and Trueb, 1994). Shine's safe harbor hypothesis posits that natural selection will favor life histories that maximize the time spent in the safest life stages (Shine, 1978). Larger eggs, with correspondingly longer development times, are affordable only when their survival is relatively high (Sih and Moore, 1993; Jørgensen et al., 2011). The safe harbor hypothesis suggests that parental care increases egg survival (*via* nest attendance or egg guarding) above the survival of a small hatchling, and, therefore, egg size will increase in populations with parental care, decreasing the duration of subsequent, higher risk stages (Wilbur, 1977a; Sargent et al., 1987; Nussbaum and Schultz, 1989; Kolm and Ahnesjö, 2005; Summers et al., 2006, 2007; Schulte et al., 2020). In the absence of parental care, egg safety is predominantly controlled *via* egg-deposition site (Petranka and Petranka, 1981; Petranka, 1990; Shine and Harlow, 1996; Mitchell, 2002; Martin and Carter, 2013; McKeon and Summers, 2013). Consistent with the theory, viviparity (the retention of offspring *in utero*) is more prevalent in regions where external eggs would experience lethally high nest temperatures, or cold climates that would slow offspring development (Shine et al., 2003; Ma et al., 2018), and high predation environments can trigger early hatching in several amphibian species (Warkentin, 2011).

Nussbaum (1987) challenged the safe harbor hypothesis by suggesting egg size in amphibians is determined by bottom-up (food availability) as opposed to top-down (predation) forces, and parental care in stream salamanders reflects a consequence of large eggs, rather than the reverse. The contrasting effects

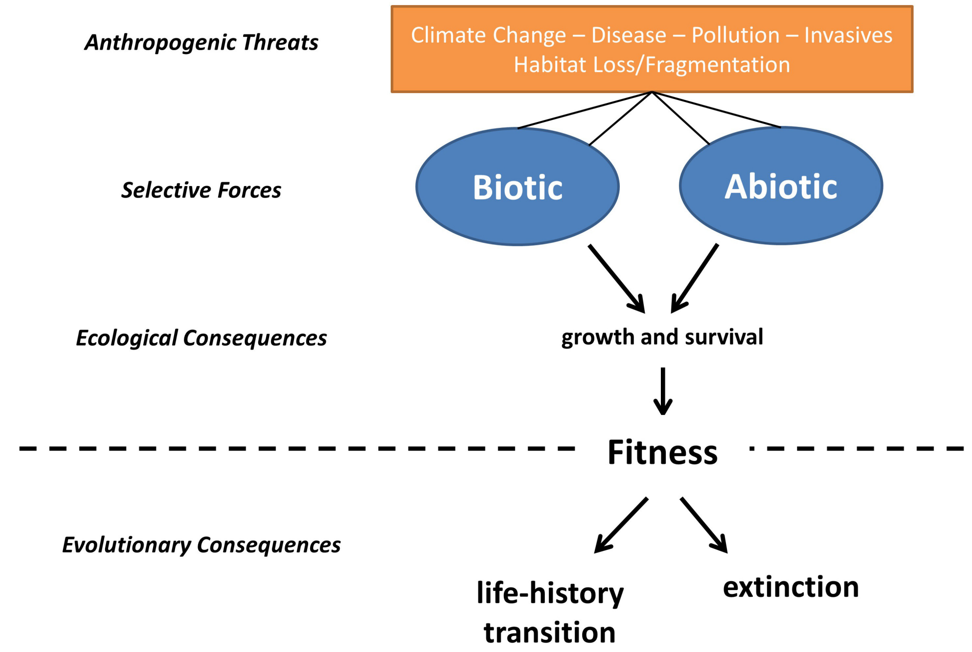

FIGURE 1 | The predicted consequences of anthropogenic stressors on the selection of life-history strategies, adapted from Southwood (1988). The strategy selection system assumes life history strategies are shaped by particular characteristics of a given environment, such that if anthropogenic change alters the abiotic and biotic pressures experienced in that environment, a new optimal life-history strategy will emerge. In the context of amphibian life-histories, changes that disproportionately impact aquatic or terrestrial environments will select for the elimination of the aquatic or terrestrial phase in a life-cycle and/or render species with particular life histories more vulnerable to extinction.

that resource availability and predation pressure exert on life histories has been well established (Werner and Gilliam, 1984; Berrigan and Charnov, 1994; Perrin, 1995; Sevenster, 1995; Abrams and Rowe, 1996; Arendt and Wilson, 1999; Pepin et al., 2003; Urban, 2007, 2008). Yet ultimately, a combination of top-down and bottom-up effects shape an organism's life history, making it challenging to parse out the relative contributions of each selective force (Hutchings, 1993; Stamps, 2007; Dmitriew, 2011; Fiksen and Jørgensen, 2011; ten Brink et al., 2019, 2020).

The separation of life stages among habitats can lead to differences in the risk and fitness payoff (in terms of survival or reproduction) in each stage (Werner et al., 1983). In certain instances, benefits conferred *via* increased growth (g) justify spending more time in a dangerous life-stage, whilst in others, high predation risk (μ) will favor strategies that opt for slower growth in safer habitats (Werner and Hall, 1988; Lima and Dill, 1990; Ludwig and Rowe, 1990; Skelly and Werner, 1990; Rowe and Ludwig, 1991; Werner and Anholt, 1993; Relyea, 2001; Sih et al., 2004). The ratio μ/g has been used to predict transitions among life stages in different contexts (Werner et al., 1983). This ratio has been used to explain the classic amphibian life-cycle using such a risk/reward trade-off, whereby food is more abundant in water, but predation risk is likely to be higher (Wilbur and Collins, 1973; Werner, 1986), such that individuals prioritize growth in the early stages of life and survival post-metamorphosis. Metamorphosis is predicted to occur therefore, when the growth benefits no longer outweigh the mortality costs of remaining in the water (Wilbur, 1980; Werner, 1986; ten Brink et al., 2020). Intuitively this transition tends to coincide with maturity when resources start to be diverted away from growth and allocated toward reproduction, but this relationship appears somewhat flexible (Rowe and Ludwig, 1991). We propose combining this insight with Shine's original hypothesis by considering the quality of the harbor not just by its relative safety, but also by its growth potential.

VARIATION WITHIN THE CLASSIC AMPHIBIAN LIFE-CYCLE IS CONSISTENT WITH THEORY

The duration of the terrestrial stage relative to the aquatic stage varies considerably across amphibian taxa (Werner, 1986; Duellman, 1989). Differences between species emerge as a result of variation in the pressures experienced by aquatic larvae relative to the terrestrial environment they will subsequently occupy (McKeon and Summers, 2013). Amphibians that breed in lentic and lotic waterbodies exhibit consistent differences in egg size, larval morphology, and larval duration; differences predominantly driven by the predator communities and productivity/resource availability of each habitat (Salthe, 1969; Summers et al., 2007; Wells, 2007; Davenport and Summers, 2010). The reliability of waterbodies (permanent vs ephemeral) used by amphibians for breeding will also contribute to the relative safety of the aquatic environment, and thus impact reproductive strategy and larval traits (Semlitsch and Wilbur, 1988). If aquatic environments offer reduced mortality risk and high growth potential relative to the terrestrial surroundings, the aquatic stage will be long; in risky, resource-poor aquatic environments, the larval stage will be brief.

Many amphibians breed in ephemeral waterbodies, and are thus precluded from an extended larval duration (Wilbur and Collins, 1973; Werner, 1986; Wells, 2007). The absence of predatory fish can result in reduced larval mortality but the small size of most ephemeral waterbodies results in high levels of competition. Within populations, the timing and size at metamorphosis can vary due to competition and density-dependent growth rates (Wilbur and Collins, 1973; Wilbur, 1977b, 1980; Rowe and Ludwig, 1991). The detrimental effects of crowding become more pronounced as water levels recede and drought can result in 100% mortality if waterbodies dry out before larvae reach sizes necessary for metamorphosis (e.g., Taylor et al., 2006).

In ephemeral wetlands, the duration of the wet periods can be short and/or unpredictable, shaping the life histories of amphibians that breed exclusively in them. The larvae of such species occupy an environment with an intense disturbance regime, akin to ruderal plant species in Grime's life-history triangle (Grime, 1977), or opportunistic species in similar frameworks for categorizing fish life histories (**Figure 2**; Winemiller and Rose, 1992). Amphibian species in ephemeral habitats typically show rapid growth and development in order to exploit the temporary conditions (Abrams and Rowe, 1996; Altwegg, 2002; Rudolf and Rödel, 2007). Growth and development rates are also known to be extremely plastic in these species, responding to predation threats, food availability, the strength of intraspecific competition, and pond drying rates (Wilbur and Collins, 1973; Wilbur, 1977b, 1980; Werner and Gilliam, 1984; Semlitsch and Wilbur, 1988; Rowe and Ludwig, 1991; Arendt and Wilson, 1999; Urban, 2007, 2008; Dmitriew, 2011).

Whilst the larvae of ephemeral pond breeders all adopt similar strategies, adult traits differ across amphibian clades. As a rule, ephemeral pond-breeding frogs exhibit short life-spans, large clutch sizes, and high dispersal rates. These species overcome the unpredictability of larval habitats by selecting breeding locations according to environmental conditions, in line with an opportunistic or episodic strategy. Salamanders and caecilians in contrast, exhibit traits more in line with stress-tolerant or competitive strategies as adults. As the unpredictability of larval habitat increases, salamanders tend towards longer lifespans that incorporate relatively low annual reproductive investment and multiple breeding attempts. Such a strategy is possible owing to their fossorial existence following metamorphosis and the stability of their underground retreats. The reduced dispersal abilities of salamanders and caecilians compared with frogs and toads may help to explain the relative proclivity of these clades to evolve direct development, whereby eggs are deposited terrestrially and hatch into miniature adults. Without the ability to disperse among breeding locations when conditions at a given site are unsuitable, many have evolved a life history that omits the aquatic stage entirely (Wilbur, 1980; Martin and Carter, 2013). More generally, when the risk-reward trade-off is perpetually favorable in one environment, direct development or paedomorphic strategies will emerge (**Figure 3**).

DEVIATIONS FROM THE CLASSIC AMPHIBIAN LIFE CYCLE ARE CONSISTENT WITH THEORY

Most salamanders and caecilians deposit their eggs terrestrially (Wake and Hanken, 2004). Although predation rates are generally thought to be higher in aquatic environments, terrestrial eggs will only achieve higher survival rates compared with aquatic eggs if they are not at risk of desiccation

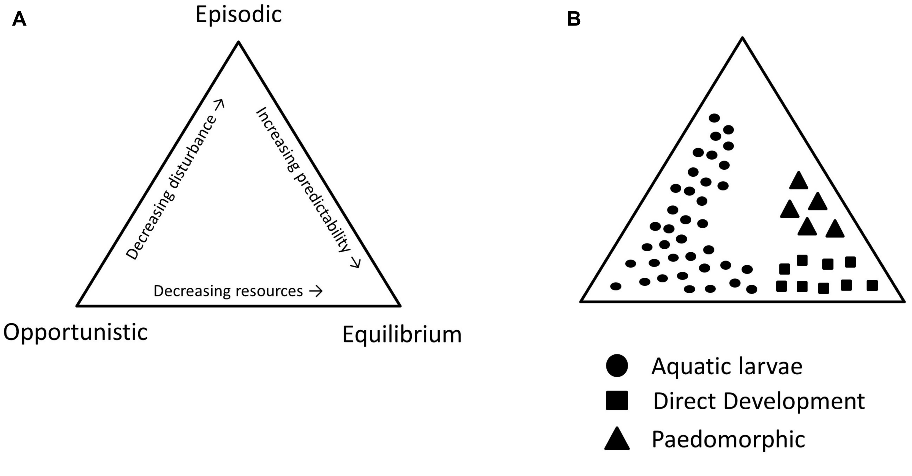

FIGURE 2 | (A) Reproduction of the life-history classification system of Winemiller and Rose (1992). A species' position within the triangle is determined by features of the environment; selection pressures include resource abundance, disturbance regimes, and environmental predictability. **(B)** Assumed position of life-history strategies for amphibians with aquatic larvae (circles), direct development/viviparity (squares), and paedomorphosis (triangles), based on species age at maturity, fecundity, and juvenile survivorship. Trait data from paedomorphic and direct developing species are scant, so we have presented the hypothetical schematic here.

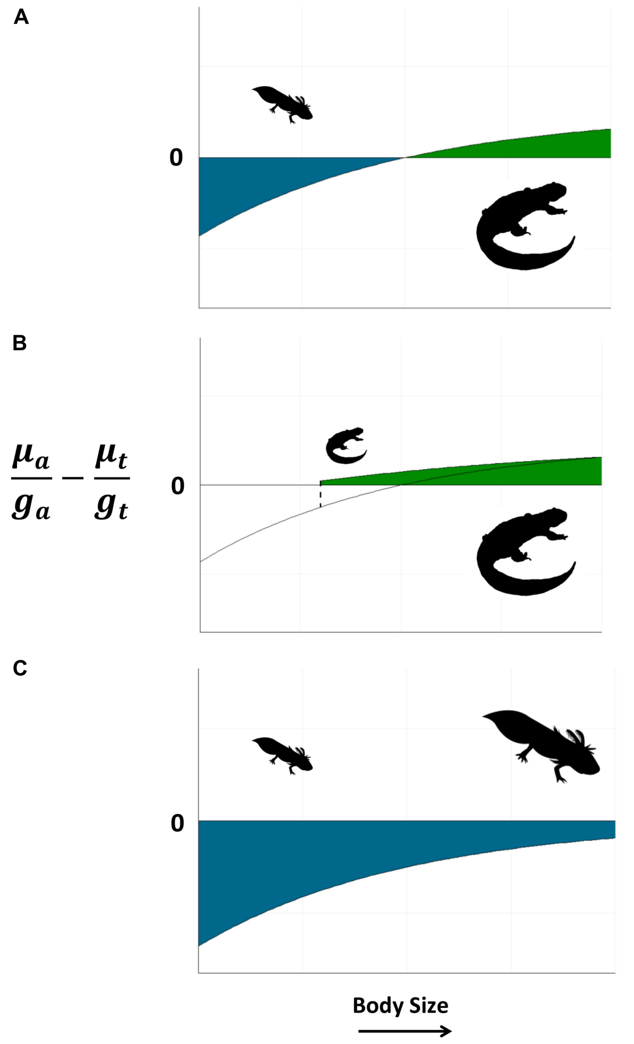

FIGURE 3 | Differences in the expected risk vs growth potential between aquatic (a) and terrestrial (t) habitats change as a function of body size, and can be used to understand the evolution of different amphibian life histories and transitions between habitats. Adapting the approach taking by Werner et al. (1983) we have plotted a horizontal line where the trade-off between mortality (μ) and growth (g) in each habitat is equivalent, $\frac{\mu_a}{g_a} = \frac{\mu_t}{g_t}$. Below this line, we expect the aquatic environment to be more favorable and vice versa for the terrestrial environment. **(A)** Illustrates a version of the classic amphibian life cycle, where this framework can predict the optimal size at metamorphosis. In **(B)** the aquatic stage is lost in favor of direct development and parental care, which increases the safety of the terrestrial stage above the scenario depicted in **(A)**. In **(C)** we illustrate a paedomorphic species in which the terrestrial stage is lost and species retain gills and remain in aquatic habitats throughout their lives.

(Martin and Carter, 2013). Direct development is therefore associated with small clutches of large eggs (Salthe, 1969; Salthe and Duellman, 1973; Summers et al., 2007; Silva et al., 2020) and far more prevalent in the humid tropics (Duellman, 1989, 1999; Haddad and Prado, 2005; Martin and Carter, 2013; Lion et al., 2019). The environments that many direct developing species inhabit are relatively stable and resource poor, selecting for equilibrium strategists (**Figure 2**).

There is also a strong correlation between direct development, duration of the egg stage, and parental care (Petranka, 1998; Kolm and Ahnesjö, 2005; Summers et al., 2006, 2007; Martin and Carter, 2013; Vági et al., 2019, 2020). Direct development enables the evolution of parental care by bringing parent and offspring into the same environment, and is expected to be advantageous given the ability of adults to keep eggs hydrated (Duellman, 1989; Bickford, 2004; Delia et al., 2013; Martin and Carter, 2013; Poo and Bickford, 2013; Schulte et al., 2020; Vági et al., 2020). Further, nest attendance can protect terrestrial eggs from would-be predators (Tornik, 2010; McKeon and Summers, 2013; Poo and Bickford, 2013) or fungal infections (Green, 1999; Schulte et al., 2020; Vági et al., 2020).

Frogs and salamanders that exhibit terrestrial egg deposition yet retain the aquatic larval stage show similarities to species with direct development, with comparable reductions in clutch size and a proclivity for parental care (Salthe and Duellman, 1973; Martin and Carter, 2013; Chuang et al., 2017; Schulte et al., 2020). This observation conforms to theoretical expectations given that the risk-reward trade-off for eggs and larvae in aquatic habitats is markedly different. Safety is the only concern for eggs, hence terrestrial egg deposition is typically favored (if eggs can be kept hydrated), but upon hatching, growth potential must be taken into consideration, leading to the retention of aquatic larvae in several clades. Alternatively, larvae may be more effective at ameliorating predation risk compared with eggs; anti-predator behavior in amphibian larvae is well documented (Wells, 2007).

Viviparity lies at the extreme of parental investment, and is similar to direct development in that it eliminates the aquatic life stage and severs an amphibian's ties with the water. Among amphibian orders, viviparity is most common in caecilians; limblessness and a fossorial lifestyle both ameliorate the high costs of egg retention and post-parturition care (Brodie, 1989; Kupfer et al., 2016). As with direct development, viviparity also appears to be related to the availability and profitability of freshwater habitats. *Salamandra salamandra* has a widespread distribution covering western and central Europe with considerable reproductive diversity (including egg-laying and viviparity) across its range, but live-birth is only exhibited in populations on islands that lack surface water for larval development (García-París et al., 2003). The aridity of the region appears to preclude direct development of eggs (Velo-Antón et al., 2007).

The paucity of viviparity in anuran clades can be explained by the fact that most frogs and toads have external fertilization, precluding a choice between live birth and egg deposition (Townsend et al., 1981; Beck, 1998; Schulte et al., 2020; but see Kühnel et al. (2010)). Of the handful of species that do exhibit internal fertilization, however, many give birth to fully developed froglets/toadlets (Wake, 1978, 1980; Beck, 1998), and one recently described species gives birth to live tadpoles (Iskandar et al., 2014). It has been hypothesized that external fertilization is common in most anurans and may facilitate the evolution of paternal care (Gross and Shine, 1981; Beck, 1998; Benun Sutton and Wilson, 2019). The high relative clutch mass of frogs and toads may preclude extensive parental care from the mother in most instances, selecting for alternative strategies. Of note, several live-bearing and "pseudo" live-bearing species (e.g., gastric brooding frogs) have already gone extinct (Blaustein et al., 1994; Iskandar et al., 2014).

Paedomorphism, the process of retaining larval features and developing a fully aquatic lifestyle, is restricted to salamanders. Within a species, paedomorphic and metamorphic populations can occur (Semlitsch et al., 1990; Denoël and Joly, 2001). This unique ability to facultatively alter development offers a chance to understand the selection pressures favoring each morph. Paedomorphism may simply reflect a novel form of resource partitioning if intraspecific competition is reduced when both paedomorphic and metamorphic strategies co-occur (Semlitsch, 1987; Denoël and Joly, 2001), but relative predation pressures on land and in the water, water availability, dispersal limitation, aquatic breathing, terrestrial habitat suitability, and anti-predator refuges have all been shown to influence the ratio of paedomorphs to metamorphs in sympatric populations (Semlitsch, 1987; Jackson and Semlitsch, 1993; Denoël and Ficetola, 2014). In other species with facultative paedomorphosis, there is a tendency for paedomorphic populations to occur in arid regions and at high altitudes, suggesting that environmental pressures on land (extreme temperatures or UV exposure) are selecting for the elimination of the terrestrial stage, physiology permitting (Wells, 2007; Trumbo et al., 2013).

For paedomorphism to evolve, breeding activities must occur in permanent waterbodies (Denoël et al., 2005; Winandy et al., 2015). Of the handful of amphibians that exhibit obligate paedomorphism, most are notably large-bodied species that have presumably evolved to exploit the high growth potential of their aquatic habitats in order to outgrow gape-limited aquatic predators. All four obligate paedomorphic salamander lineages (Cryptobranchidae, Sirenidae, Amphiumidae, and Proteidae) exhibit extensive parental care (Petranka, 1998), indicating that the aquatic environments in which they are found can only be inhabited if the survival of early life-stages can be effectively increased. Paedomorphism may also confer a reproductive advantage both through being able to exploit the productive aquatic environment throughout life, and by avoiding the energetically costly process of metamorphosis (Semlitsch, 1985). In tiger salamander populations, paedomorphic individuals have larger clutches than metamorphic individuals (Whiteman, 1994; Sagar et al., 2007).

CONSERVATION STATUS OF AMPHIBIANS WITH DIFFERENT LIFE HISTORIES

Amphibians continue to show the steepest population declines of any vertebrate clade (González-del-Pliego et al., 2019), and are faced with numerous, often cumulative, threats (Kiesecker et al., 2001; Collins and Storfer, 2003; Stuart et al., 2004; Sodhi et al., 2008; Pabijan et al., 2020). The relative time spent in aquatic and terrestrial life-stages determines the identity and severity of threats posed to amphibian taxa. In addition, the traits that characterize different amphibian life-history strategies are predicted to influence species' susceptibility to anthropogenic threats, such that species with "faster" life histories are more likely to recover from declines (Pimm et al., 1988; Bennett and Owens, 1997; Hutchings et al., 2012; Pincheira-Donoso et al., 2021). Accordingly, threat status on the IUCN Red List has been related to mode of fertilization (internal vs external), clutch size, egg deposition site, and degree of parental care in several taxa (Hero et al., 2005; Bielby et al., 2008; Sodhi et al., 2008; González-del-Pliego et al., 2019; Pincheira-Donoso et al., 2021).

By relating IUCN threat status with reproductive modes obtained from a global amphibian trait database (Oliveira et al., 2017), we find that direct developers are faring poorly when compared with species exhibiting aquatic larval stages in their assessments (**Figures 4**, **5**). Furthermore, many live-bearing species are Data Deficient on the IUCN Red List (**Figures 4**, **5**), but have been predicted to be more threatened than those already assessed (Howard and Bickford, 2014; but see Bielby et al. (2006)). In other words, the life histories that have the "safest harbors" appear to be in the greatest danger.

That a greater proportion of terrestrial amphibian species are currently threatened with extinction may be a counter-intuitive conclusion to some, given that many of the major threats to amphibians (e.g., disease, pollution, and habitat loss) disproportionately affect species with aquatic larvae (**Table 1**). The small number of paedomorphic species prevents a similar comparison; it can be safely assumed, however, that the predominant threats to paedomorphic populations will be more similar in nature to those faced by species with aquatic larvae than those faced by fully terrestrial amphibians. Thus it seems that paedomorphic species do not appear to be faring as poorly as those with viviparity and direct development. To explore these disparities in more detail, we discuss the major threats to amphibians in the context of each life-history strategy and the ecological drivers that contribute to a species' extinction risk.

Habitat Loss

A large body of previous work established habitat loss and degradation due to land use change as the primary threat to amphibian diversity. Wetlands are being lost three times faster than forests are being cleared (Wood et al., 2003), with lentic waters (lakes) also suffering heavy losses and degradation (Ricciardi and Rasmussen, 1999; Dudgeon et al., 2006; Liermann et al., 2012; Reid et al., 2019). The elimination of permanent wetlands or changes in the drying regime of ephemeral pools, in addition to pollution, invasions, or thermal changes, will disproportionately affect species that spend all or part of their life in water (Lips et al., 2003; Lion et al., 2019). The Least Concern status of many amphibians with aquatic larvae therefore remains puzzling, and may simply reflect particular biases in the way species are evaluated (Bielby et al., 2006; Becker and Loyola, 2008; Loyola et al., 2008; Becker et al., 2010).

Habitat change varies by continent and habitat type, and could affect species with different geographic ranges differently. Species with small geographic ranges have been shown to be more at risk of extinction, both on theoretical grounds and in reality (Hero et al., 2005; Payne and Finnegan, 2007; Cooper et al.,

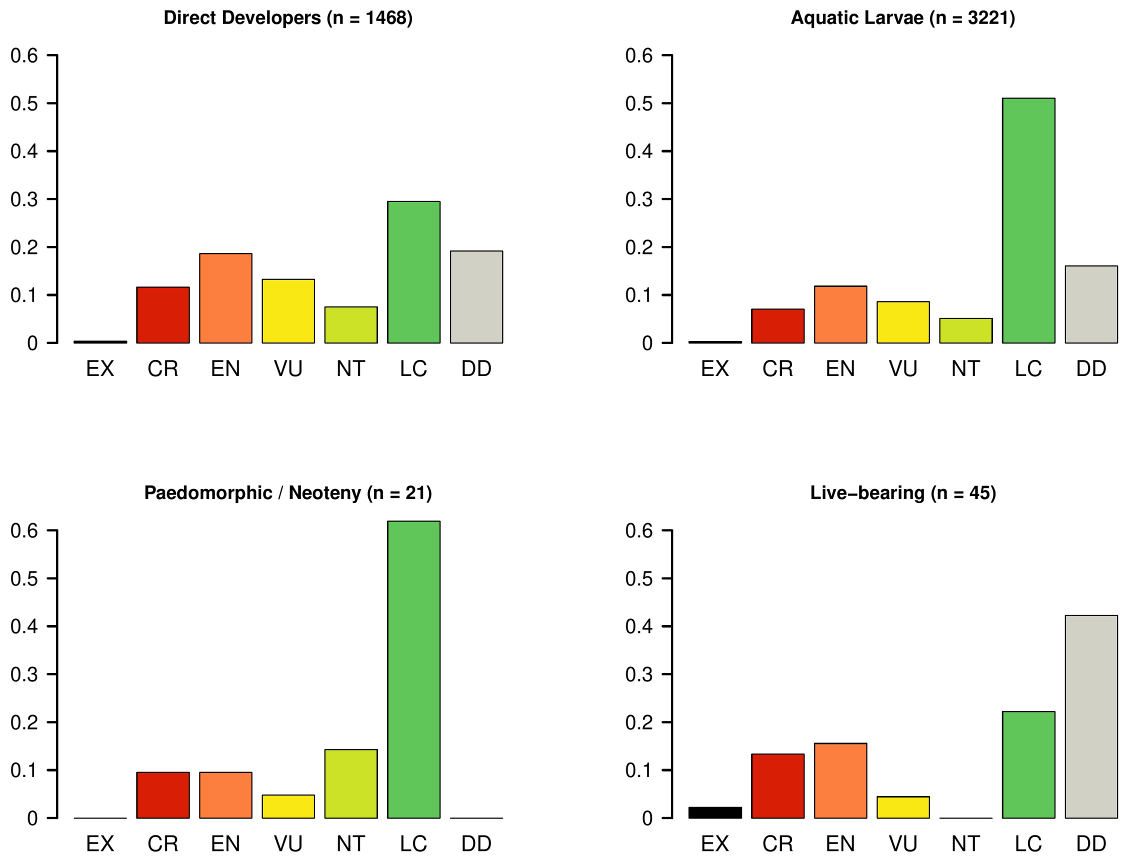

FIGURE 4 | IUCN Red List status of all amphibians by major life-history strategies. The height of each bar corresponds to the percentage of the group in each Red List status category (EX, extinct; CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern; DD, data deficient).

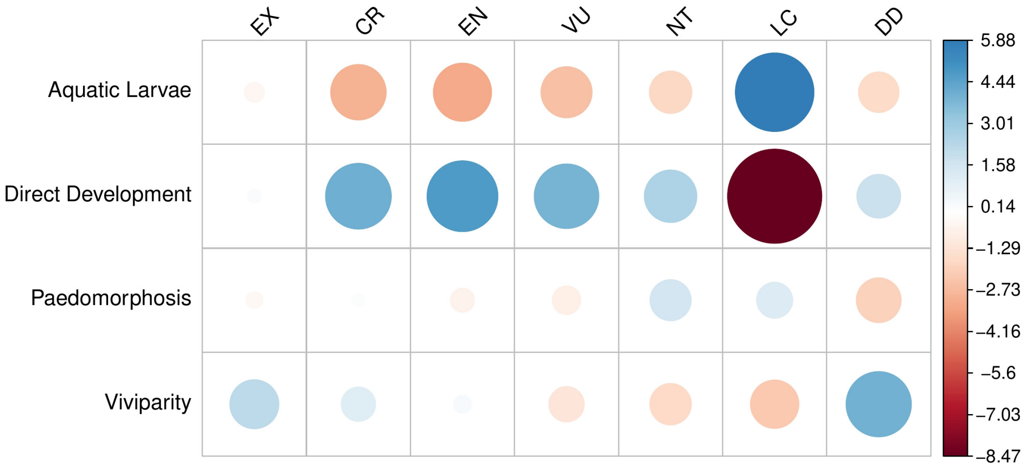

FIGURE 5 | Disparities in conservation status of amphibian life-history strategies (χ^2 = 242.64, df = 18, *p*-value < 2.2e–16). Size and color of points are scaled to Pearson's residuals. Warm colors indicate groups with fewer species expected by chance; cool colors indicate groups with more species than expected.

2008; Sodhi et al., 2008; Smith and Almeida, 2020). Terrestrial species tend to have smaller geographic ranges, perhaps making them more susceptible to habitat loss and stochastic extinction in general (Cooper et al., 2008; Sodhi et al., 2008). Further, many terrestrial amphibians are restricted to tropical regions and mountain ranges, where current threats to intact habitat are most

TABLE 1 | Threats posed to amphibian taxa according to the International Union for Conservation of Nature (IUCN) as of January 2021.

	Urban development (%)	Agriculture (%)	Energy production (%)	Roads (%)	Biological resource use (%)	Human intrusions (%)	Natural system modifications (%)	Invasive and diseases (%)	Pollution (%)	Geological events (%)	Climate change (%)
Direct development (*n* = 1,114)	41	79	11	6	67	8	18	29	15	3	13
Aquatic larvae (*n* = 2,294)	45	73	9	8	62	5	23	32	32	1	8
Paedomorphic (*n* = 17)	65	29	24	35	29	12	35	18	65	0	12
Viviparous (*n* = 35)	49	54	6	9	60	3	37	11	23	0	6

Values represent the proportion of species within each life-history category judged to be impacted by each corresponding threat.

serious (Duellman, 1999; Haddad and Prado, 2005; Lion et al., 2019). Whilst a biogeographical explanation for the observed patterns we see is appealing and intuitive, it fails to explain much of the difference in threat statuses across amphibian clades (Bielby et al., 2006). Thus we must also consider life history as a plausible explanation for these observed differences.

Theory predicts that a species' life history will interact with habitat alterations to determine extinction risk. For example, terrestrial species presumably have evolved parental care, viviparity, or direct development to increase the safety of early life stages. Increased investment per offspring, however, will only be favored if variability in offspring survival is low or can be sufficiently dampened through behavioral means. Thus these strategies are largely restricted to relatively stable environments (Duellman, 1989; Vági et al., 2020). In contrast, the unpredictability of many pond and wetland habitats typically favors high dispersal capabilities, shorter life spans, and larger clutches of small eggs (Green, 2003; Wells, 2007; Semlitsch, 2008; Bonte and Dahirel, 2017). These traits are all associated with an opportunistic breeding strategy that equips populations with a life history that is naturally adapted to persist under anthropogenic stress (Duellman, 1989; Green, 2003; Kindsvater et al., 2016; Allen et al., 2017).

Disease and Invasive Species

Susceptibility to the introduction of non-native species and/or novel pathogens will be strongly dependent on life history. When considered globally, the most devastating amphibian diseases are water-borne (e.g., chytrid fungus and ranavirus), and could disproportionately imperil species with aquatic larvae (Lips et al., 2003; Piotrowski et al., 2004; Bielby et al., 2008; Smith et al., 2009; Scheele et al., 2014). Fungal pathogens, however, appear to impose challenges to the eggs of both aquatic and terrestrial species (Green, 1999; Pounds et al., 2006; Schulte et al., 2020). Although exposure risk to water-borne diseases such as chytridomycosis and *Batrachochytrium salamandrivorans* is reduced, terrestrial species may have lower resistance to these pathogens (Mesquita et al., 2017). Indeed, the large eggs of direct developing species are more susceptible due to the longer duration of the egg stage, and the care of eggs (such as brooding) seen in many terrestrial amphibians is thought to be related in part to preventing fungal infection (Green, 1999). Skin secretions from attending parents have been shown to confer pathogen resistance to clutches (Schulte et al., 2020 and references therein), and the high incidence of parental care in all three amphibian orders suggests disease may often play a crucial role. More investigation is needed as to the link between amphibian life histories and susceptibility to disease.

Although less well studied, invasive species will drastically alter the relative safety of aquatic and terrestrial habitats in similar fashion to novel pathogens (Winandy et al., 2015). When sympatric populations of paedomorphic and metamorphic newts are confronted with an introduced predator (stocked fish), the fully aquatic, paedomorphic populations are much more likely to be driven to extinction (Denoël et al., 2005; Pope, 2008). Species with facultative paedomorphosis may be able to persist with merely an alteration in the numbers of paedomorphic and metamorphic individuals, but for most taxa invasions will pose a more serious threat (Winandy et al., 2015). If the pressures brought by invasive predators and/or competitors render the aquatic environment completely uninhabitable, fully terrestrial strategies are unlikely to evolve in time (ten Brink et al., 2019, 2020).

Climate Change

Predicting the impact of climate change will be most difficult for species with multiple life stages that respond differently to rapid shifts in environmental conditions (Kingsolver et al., 2011; Levy et al., 2016). Amphibians' vulnerability will be mediated by the relative time spent in aquatic and terrestrial habitats, and the susceptibility of each stage to alterations in temperature and precipitation regimes. A simple prediction is that aquatic species or life stages will be buffered from environmental perturbations owing to the thermal inertia of water (Martin and Carter, 2013). The environmental conditions at some amphibian breeding wetlands, however, are predicted to become unsuitable with changing precipitation regimes (e.g., Chandler et al., 2016; Lertzman-Lepofsky et al., 2020). Particularly for species that breed in ephemeral wetlands, climate change may shorten hydroperiods, preventing larvae from completing development, or increase the frequency of fish predators being washed in following major storm events. Phenological mismatches are another concern for pond-breeding amphibians. Unless species can adjust the timing of seasonal migrations to fit new rainfall patterns, or relocate to neighboring wetlands with more appropriate hydrological characteristics, successful breeding bouts will become increasingly rare.

Range shifts in response to climatic warming are predicted for many taxa, yet it remains unclear as to what degree amphibians will be able to keep pace with rapid environmental change and relocate to higher altitudes or latitudes (Forero-Medina et al., 2011; Li et al., 2013; Trumbo et al., 2013; Lion et al., 2019). Although we must always consider the possibility that our understanding of dispersal is biased by the difficulty in documenting inter-patch movements (Smith and Green, 2005; Denoël et al., 2018), amphibians as a group appear to have limited mobility (Semlitsch and Bodie, 2003; Pabijan et al., 2020). Low dispersal ability relative to other vertebrates, coupled with strong site fidelity, will certainly heighten amphibians' susceptibility to climate change (Travis et al., 2013). Although no data for caecilians exists, differences in dispersal capabilities and site fidelity appear pronounced between frogs and salamanders (Semlitsch and Bodie, 2003; Smith and Green, 2005). A more solid theoretical framework of amphibian dispersal syndromes is needed to assess the relative vulnerability of the three orders (Buoro and Carlson, 2014; Bonte and Dahirel, 2017).

In the context of developmental modes, dispersal in amphibians occurs almost exclusively in the terrestrial phase (Wilbur and Collins, 1973; Wilbur, 1980; but see Pašukonis et al. (2019)). Paedomorphic species in lentic waters have no dispersal capabilities, and are thus at the mercy of a changing climate. The situation is equally problematic for mountain-top and island endemics, a high proportion of which exhibit direct development (Bielby et al., 2008; Forero-Medina et al., 2011; Lion et al., 2019; Lourenço-de-Moraes et al., 2019, 2020). Further, if direct development is intrinsically linked to small geographic ranges, even species not confined to montane environments may lack the mobility to track viable climatic envelopes (Lion et al., 2019; Lourenço-de-Moraes et al., 2019, 2020). Our understanding of amphibian movement is limited and as such the link between life-history strategy and dispersal remains unclear, yet such matters carry strong implications for a species susceptibility to anthropogenic threats (Lourenço-de-Moraes et al., 2019, 2020; Pabijan et al., 2020).

Last Resort Interventions

For some amphibians, the threat of extinction is so serious that captive breeding populations have already been established to minimize the chance to stochastic extinction in the wild. Species with elaborate parental care or complex life cycles are likely to present the greatest challenge with regard to husbandry and captive rearing efforts (Tapley et al., 2015). Further, the commercial importance of species, whether farmed for food or popular in the pet trade, will also have a strong bearing on the speed at which a successful captive facility can be set up. Initiating new breeding programs will be particularly onerous for late-maturing species with small clutch sizes (Elinson et al., 1990; Mohanty and Measey, 2019), and this describes many of the fully terrestrial clades with direct development or viviparity. Several paedomorphic lineages also take multiple years to reach sexual maturity, but their larger clutches and popularity as food or pets may alleviate the difficulties in building captive colonies.

The success of reintroduction efforts is directly correlated with the number of animals released to establish new populations (Germano and Bishop, 2009). Generating the quantity of animals required for reintroductions to represent a viable strategy will take much longer for terrestrial species (Tapley et al., 2015; Harding et al., 2016). The situation is similar when considering translocations of amphibians to areas that are expected to be more hospitable following climate change (assisted dispersal). Translocations attempts will be considerably more challenging for species with direct development, yet it is likely that these species are most in need of such drastic interventions (Tapley et al., 2015). Lastly, it is important to recognize that captive rearing is only a temporary stop-gap that does not address the factors that caused declines in wild populations (Griffiths and Pavajeau, 2008; Scheele et al., 2014; Harding et al., 2016; Pabijan et al., 2020). The ability to eradicate diseases or the time it takes to restore habitats will need to be balanced with the difficulties associated with keeping animals alive in captivity and generating the numbers necessary to attempt reintroductions (Griffiths and Pavajeau, 2008; Scheele et al., 2014; Pabijan et al., 2020).

CONCLUDING REMARKS

Global amphibian declines have gained increasing recognition and attention, but understanding species' trajectories in the context of their differences in life history is a thorny problem. To address this gap, we have brought to bear classic theory that describes and predicts life-history strategies the safe harbor hypothesis, μ/g, and C-S-R on the intractable problem of understanding why certain amphibian species are threatened with extinction, and others are, to date, of Least Concern.

In the face of multiple threats, and the fact that knowledge of amphibian species richness is still limited – and most species lack basic life-history data on clutch number, lifespan, or other important demographic traits – conservation efforts for amphibians cannot take a one-size-fits-all strategy. We suggest that our framework of risk-reward trade-offs to explain diversity in amphibian life histories – notably developmental and reproductive modes – can offer insights into the distribution of threat status across the tree of amphibians. The complete elimination or addition of a life-history phase to compensate for rapid anthropogenic alterations to aquatic and terrestrial environments appears unlikely; in most instances species with particular life histories will simply go extinct (ten Brink et al., 2019, 2020).

Amphibians with direct developing and viviparous life histories are (proportionally) at greater risk of extinction. The safe harbor provided by mothers of these species may, unfortunately, generate a life history that is intrinsically more sensitive to anthropogenic stressors. The intrinsic connections between developmental mode, clutch size, species range size, and biogeography often put terrestrial species at greater risk (Lion et al., 2019; Pincheira-Donoso et al., 2021). The inherently unpredictable nature of aquatic environments and instability of complex life cycles (Istock, 1967) produces more of a bet-hedging strategy in classic amphibians that may serve them well in light of anthropogenic change. The situation reminds us of Alfred Crosby's take on the progress of civilization, "Specialization almost always narrows the possibilities for future change: for the sake of present convenience, we loot the future."

We suggest there is a role for basic research, focused on species with facultative transitions between paedomorphic and metamorphic lifestyles, or egg laying and viviparity, to gain a deeper understanding of mortality schedules and ecological drivers of life-history transitions. Our theoretical framework provides a basis from which to predict the impact of multiple threats acting synergistically in the context of each life-history strategy and prioritize data deficient species about which little is known (Blaustein and Kiesecker, 2002; Silva et al., 2018). Clades in which direct development or viviparity are common are of special concern, but we cannot rule out the possibility that species with aquatic larvae are equally imperiled, and their IUCN Red List status simply reflect biases in our status assessments when evaluating species with high fecundities and large geographic ranges (Bielby et al., 2006; Harper et al., 2008; Middleton and Green, 2015; Lion et al., 2019).

We acknowledge that life histories alone will not account for all of the factors vulnerability assessments aim to capture (Bielby et al., 2006; Becker and Loyola, 2008; Loyola et al., 2008; Becker et al., 2010). However, by highlighting discrepancies in threat status and vulnerability, our approach may help to reveal species or regions where exposure to anthropogenic threats is particularly acute and where interventions are most needed. Communities in which diverse life histories are present will prove particularly useful in disentangling the contributions of exposure and innate vulnerability in determining a species' extinction risk.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: life-history data were obtained from AmphiBIO, a global amphibian trait database (Oliveira et al., 2017), and can be accessed at doi: 10.1038/sdata.2017.123. Red List categories were downloaded from the IUCN Red List of threatened species on 21st March 2021, https://www.iucnredlist.org.

AUTHOR CONTRIBUTIONS

GB and HK were involved in conceptual development, writing, and editing. GB performed the statistical analyses and created the figures. Both authors contributed to the article and approved the submitted version.

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